HAIR AND FEATHERS.

By J. S. Kingsley.

Birds and mammals, the highest groups of the whole animal kingdom, are sharply marked off from each other and from all other vertebrates by their tegumentary structures, feathers in the one group, hair in the other. Naturally structures so characteristic and evident as these have been made the subject of numerous investigations, but the more recent and more thorough studies have been published almost exclusively in German, and hence a summary of these may be acceptable to American readers. In the preparation of the following account the recent able review by Professor Keibel[1] has been freely used.

In the skin of the higher vertebrates two distinct portions may be recognized, differing in origin, structure, etc. The outer of these layers, the epidermis, arises from the ectodermal layer of the embryo, while the other layer, the cutis or dermis, has its origin in the mesoderm (mesenchyme). When fully developed the epidermis consists of a basal layer of cells resting on the dermis and receiving nourishment from it. By continual growth and consequent division, this basal layer produces other cells which come to lie outside it, but these more superficial portions, removed from any food supply, do not grow or divide, but die, dry up and become hardened into a horny cuticular layer which gradually wears away and is as constantly renewed from beneath. Outside of this cuticular layer comes a third layer, the epitrichium, only a single cell in thickness, which is lost in the mammals at a very early date, but which persists until a later stage in birds.

The deeper layer of the skin, the dermis or cutis, is largely composed of dense fibrous connective tissue, the fibres of which are tightly interlaced, and among them run nerves and

[1] Merkel und Bonnet's Ergebnisse der Anatomie und Entwickelungsgeschichte, 1896.

minute blood vessels, while here and there are developed muscle fibres of the smooth or involuntary type. This dermis is separated from the deeper tissues by a loose or aveolar connective tissue, in which fat is often developed to a considerable extent.

In the development of a hair slight differences are observable in different forms. In some the first phenomenon is the appearance of small papillæ in the dermis at the points at which hair is subsequently to be formed; in others the process of hair formation is initiated by changes in the epidermis, which only appear after the formation of the papillæ in the first mentioned types. This change consists in an elongation of the basal cells in a direction at right angles to the surface where the hair is to appear (fig. 1), the result being that the epidermis becomes slightly pushed into the dermis in these areas. Beneath these thickenings, there next follows a multiplication of dermal cells. As growth continues the inpushings increase in extent, while the dermal cells arrange themselves around the ingrowth to form a hair follicle with a slight projection, the hair papilla, at its base (fig. 2), the latter being supplied by a small capillary loop.

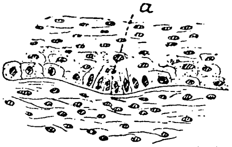

FIG. 1.—Section through the earliest stage of hair formation in a mouse, after Maurer. At *a* is shown the change in the basal layer of the epidermis.

So far the epidermal ingrowth has been solid, but now a circular depression appears, which, deepening with time, separates a central portion, the rudimentary hair, from a surrounding sheath (fig. 3). The relations will readily be seen from the illustrations, but a few words may be added to make all clear.

In figure 3 the hair is shown as a solid structure made up, as it protrudes from the skin, of three concentric layers; a central medulla, a middle so-called cortical layer, and an outer cuticular layer. Inside the

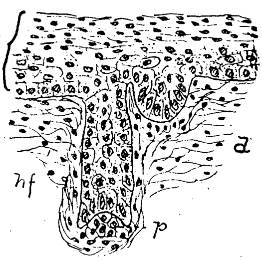

FIG. 2.—Later stages in the development of the hair in the mouse, after Maurer. On the right an earlier stage; on the left a later stage: *e*, epidermis; *d*, dermis; *hf*, hair follicle; *p* papilla.

follicle two other layers are seen, known by the names of those who first described them, the outer as Henle's layer, the inner as Huxley's layer. At one side of the follicle is shown the gland which secretes the oil, and which is clearly a derivation of the epidermis, while in several places are medullated nerve fibres connected with the sheath of the hair. The growing point of the hair is at the base of the follicle where the deeper epidermal cells, by constant division, produce other cells, which are added to the base of the hair, thus causing it continually to increase in length.

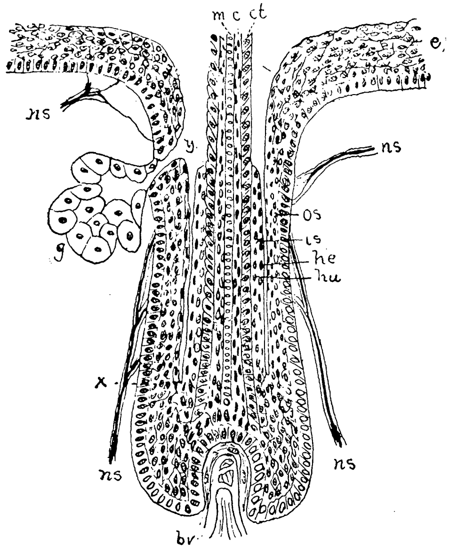

FIG. 3.—Diagrammatic section of hair and hair follicle, after Maurer. *bv*, blood vessel; *c*, cortical layer of hair; *ct*, cuticular layer; *e*, epidermis; *g*, sebaceous gland; *he*, Henle's layer; *hu*, Huxley's layer; these two composing *is*, the inner root-sheath; *m*, medulla; *ns*, secondary nerves; *os*, outer root-sheath; *x* and *y*, points regarded by Maurer as homologous with *x* and *y* of figure 13 with which this should be compared.

It may be well to say parenthetically that hair is not hollow; that the natural oil does not flow through it as through a tube, and that the singeing so strongly recommended by barbers will not close up any "openings through which the vital fluids of the hair escape."

When we look at any hairy surface the hairs appear to be arranged without any order. It is, however, interesting to note, in the light of what is to follow, that Maurer claims that the first hairs to be formed—at least in certain mammals—are arranged in a few rows, and that these rows have a definite position (fig. 4). With the later increase in the number of the hairs this regularity is lost, an intermediate stage showing the hairs arranged in groups, but it is not yet settled exactly how

much of the increase in number is to be explained by the division of hair follicles and how much by new formation. So, too, in the replacement of molted hairs it is doubtful whether a new papilla is formed, or whether the old papilla retains its functions.

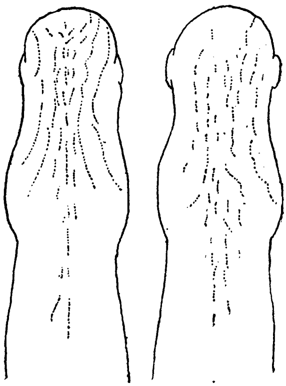

Fig. 4.—Two dorsal views of an embryo cat showing the early hair tracts. In the right hand figure the rows have been broken into patches. After Maurer.

When we analyze the phenomena of hair formation we find that the epidermis takes the initiative so far as cell multiplication is concerned. With feathers, on the other hand, the increase in cells begins in the dermis, the result being a slight elevation of the surface of the skin. Next the deeper cells of the epidermis form themselves into a double layer (fig. 5) and the whole is strikingly suggestive of a scale, in that one edge of the elevation projects more than the other. This outgrowth increases in extent until there results a cylindrical process protruding from the skin (fig. 6) with a very slight insinking, the rudiments of the future feather follicle, at its base. In this outgrowth, which is to give rise to the future down-feather, both dermis and epidermis may be recognized.

Fig. 5.—Early stage in the development of a down feathers in the pigeon. After Davies. *E*, epidermis; *ep*, epitrichium; *d*, dermis.

The epidermis has increased in thickness by cell multiplication, while the epitrichium retains its primitive condition.

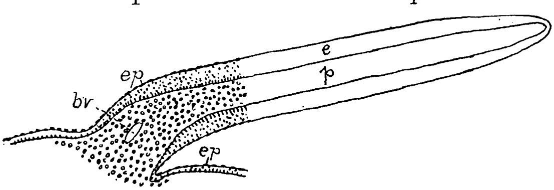

Fig. 6.—Longitudinal section of a later stage of the down feather, after Davies, *bv*, blood vessel; *e*, epidermis; *ep*, epitrichium; *p*, pulp of the papilla. The basal layer of the epidermal cells have assumed a cylindrical character.

The dermal portion, hereafter to be known as the pulp, has undergone modifications best understood by reference to a transverse section (fig. 7). It no longer has a smooth contour, but is produced in a radial manner into longitudinal ridges which nearly reach to the epitrichium. As a result of this the epidermal portion becomes divided into a corresponding number of rod-like structures, each of which becomes surrounded by a structureless ensheathing envelope produced by the basal layer of the epidermal cells.

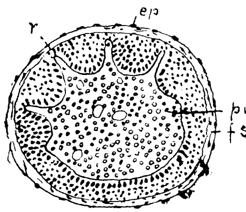

FIG. 7.—Slightly oblique section of a young down feather of a chicken near the base. After Davies. *ep*, epitrichium; *fs*, feather sheath; *pu*, pulp; *r*, ridges of the pulp dividing the epidermis into a series of rod-like structures.

The pulp now begins to retract towards the surface of the skin, leaving the whole outgrowth hollow, except for structureless partitions—the pith of the quill—here and there, produced by the retracting epidermis. The parts remaining external to surface of the body gradually dry up and become cornified, and, the epitrichial sheath breaking away, the epidermal rods just mentioned separate at their free ends, so that the well-known down-feather results, the basal, undivided portion of the outgrowth forming the small quill.

During this formation of the down-feather the follicle becomes much deeper, so that at length it presents considerable superficial resemblance to the hair follicle, and into it the dermal pulp retracts after the full formation of the down-feather is complete.

According to Davies all contour feathers are preceded by down-feathers, and even those cases which seem to form exceptions to this statement are found upon more accurate observation to accord with it. The statement may be put in another way: the germ of the definitive feather is a direct derivative of the germ of the down-feather. Let us now follow the development of a symmetrical contour feather.

With the retraction of the pulp (fig. 8) the follicle widens while the feather papilla enlarges so as to contain a much more considerable pulp, but in other respects it is closely similar to

the earlier down papilla except that it is seated in a follicle. There now occurs the same outgrowth of ridges from the pulp as before, dividing the epidermis in a similar manner, with the following exceptions: In the down papilla these ridges were parallel to the axis of the future feather; in the contour feather (fig. 9) they are oblique to that axis, the result necessarily being that the formations of a series of long slender processes—the future barbs—which are connected with an undivided portion, the shaft—on the so-called dorsal side of the papilla. Around all is developed a sheath as before.

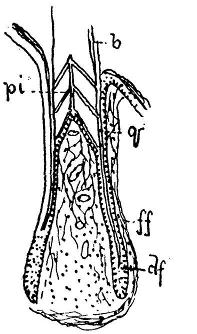

FIG. 8.—Longitudinal section through the shaft of a primary down-feather, after Davies. *b*, barbs; *df*, apex of the definitive feather germ; *ff*, feather follicle; *pi*, pith; *q*, quill.

This dorsal or shaft region demands a little closer attention. As seen in transverse section (fig. 10) the shaft shows on its inner edges longitudinal thickenings which, increasing in size, meet each other in differing ways in the different parts of the feather. A glance at figure 11 will explain this better than pages of description. The four sections are made at different levels, *A* being near the tip and *D* through the quill below the vane. Around each is the feather sheath and inside of each is the pulp cavity. In *A* the ingrowing edges of the shaft meet each other, and form a solid rod. Farther down, as in *B* and *C*, they include in the ingrowth a portion

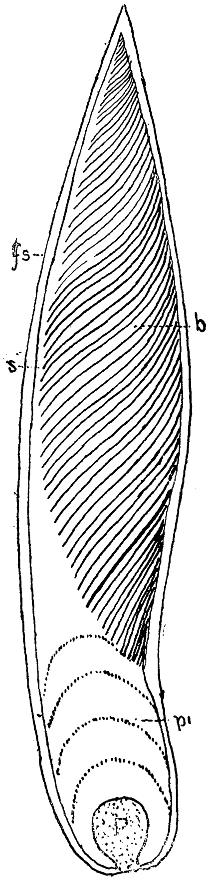

FIG. 9. — Diagrammatic representation of a definitive feather in its sheath, represented as a transparent object, after Keibel. *b*, barbs; *fs*, feather sheath; *p*, papilla; *pi*, pith; *s*, shaft.

of the pulp cavity thus making this portion of the shaft hollow; while in *D*, taken below the vane we have no barbs and only the hollow quill.

With the contour feather, as with the down feather there is the same retraction of the pulp and the same formation of pith as has already been described. After the feather is complete the retracted pulp remains quiet until about the time of the molt when it comes to the front again to form the new feather. The feather, the development of which we have been following, is as yet cylindrical in shape and is still enclosed in the feather sheath. With the retraction of the pulp it dries and becomes horny as before, the sheath breaks away and the barbs by their elasticity straighten out and become arranged on either side of the shaft (see fig. 12) so as to form the well-known vane.

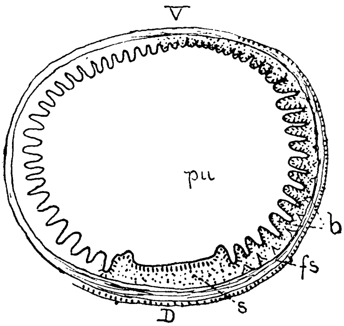

FIG. 10.—Section near the tip of a developing contour feather of a Canary, after Davies. *b*, developing barbs; *fs*, feather sheath; *pu*, pulp; *s*, sheath; *d* and *v*. dorsal and ventral.

There are here to be mentioned two points. The first is that the upper and lower surfaces of the contour feather do not

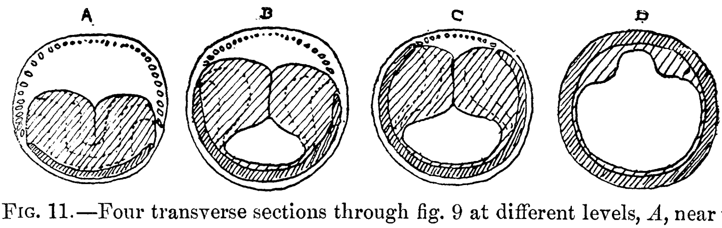

FIG. 11.—Four transverse sections through fig. 9 at different levels, *A*, near the tip; *D*, near the base.

correspond to the upper and lower surfaces of the papilla but rather to the inner and outer surfaces of the feather-forming epidermis, as may be seen by a comparison between figures 10 and 12. The other matter is this: With the withdrawal of the pulp from the feather there is no longer any nerve or blood

supply to the parts of the feather. The cells of which it is composed are dead and dry so that it seems impossible that any change can take place in it. The whole question of change in color of the fully formed feather was recently reopened by Mr. J. A. Allen who maintained that, once formed, the feathers do not change in their markings. The whole history of development seems to afford him full support. Yet this year the attempt has been made to show that feathers do change in their markings. In this, as the matter now stands, the burden of proof is upon those who support the possibility of change.

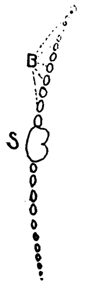

FIG. 12.—A section through a feather at the level of fig. 11A, after the rupture of the feather sheath and the spreading out of the barbs (*b*) to form the vane; *s*, shaft.

Another aspect of the hair and feather question must now be taken up. How did these two structures come into existence? They certainly were not formed *de novo*, for it is one of the axioms—we had almost said—that all structures are to be traced back as modifications of pre-existing structures. If this be so, to what can these structures be referred?

Until very recently the attempt was made to show that hairs and feathers were homologous in origin. Thus the older students sought to find intermediate stages in the pin feathers, which are certainly hair-like in appearance; and to derive both hair and feathers from the Reptilian scale, a view which received much seeming support from the tarso-metatarsal scales of birds and from the scale-like feathers of the penguins, as well as from the scaly armor of pangolins, etc., on the mammalian side. The interested student will find all of these views ably and concisely summarized by Keibel; our space will not admit more than this reference to them. It may be said, however, that Davies, to whom we owe the most accurate account of the development of the feather declines to regard pin feathers as the simplest type of the avian tegumentary covering but rather as a retrograde condition; and farther, that he regards the scales upon the tarsal and digital regions of birds as secondary formations, agreeing in this with Jeffries.

If the Mammals be, like the birds, descended from the Reptiles then it is natural that we should look for those structures which have given rise to hairs in connection with the Reptilian integument. On the other hand there are those who believe that the Mammals spring direct from some Amphibian stock and to these the recent work of Maurer is full of interest. Maurer maintains that hair and feathers are not homologous structures. The feather, according to his view has been derived from the Reptilian scale while hair has arisen from the dermal sense organs of the Ichthyopsida as a result of a change in habits and conditions of life. As illustrating his views we have copied (fig. 13) one of his figures, a diagrammatic longiudinal section of at dermal sense organ of Triton after the metamorphosis, which should be compared with the diagram of the structure of the hair follicle and hair already given (fig. 3) the letters in each indicating the homologies recognized by Maurer.

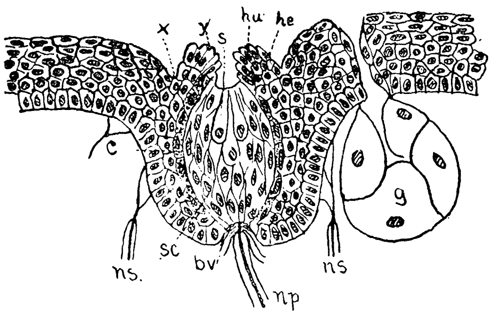

FIG. 13.—Diagrammatic section of a cutaneous sense organ of *Triton cistatus* after the metamorphosis; to be compared with fig 3. After Maurer. *bv*, blood vessel; *c*, cortical layer; *g*, gland; *he*, Henle's layer; *hu*, Huxley's layer; *np*, primary nerve; *ns*, secondary nerves; *s*, sense cells; *sc*, supporting cells, *x* and *y*, points regarded as homologous with *x* and *y* in fig. 3.

Slightly condensing his account, Maurer says, that when an Amphibian, like Triton after the metamorphosis, takes to the land, the supporting cells of the sense organs undergo a process of cornification and in this condition they show in the simplest form all of the parts of the hair and the hair follicle. With the transfer to land, as is well known, the dermal sense organs lose their original function, itself dependent upon the presence of water as a surrounding median. In the axis of the hair lies the medulla, consisting of dry incompletely cornified cells. In these I recognize the modified remains of the sense cells.[2] The cortical layer is derived from the horny

[2] A view considerably different from those earlier advanced by him.

supporting cells and the cuticula from the enveloping cells of the dermal sense organs. In the epithelium around the sense bud both Henle's and Huxley's layers may be seen forming the inner root sheath as in the hair; while the connective tissue envelope forms a sense bud follicle just as the same layer forms the hair follicle. Even a papilla is frequently present in many Amphibia; (e. g., Cryptobranchus), containing a capillary network; but since the hair has lost its sensory function the axial nerve of the sense organ has degenerated.

We cannot go into the wealth of fact and comparison which Maurer has advanced in support of his position (which we may say in passing, has won the acceptance of Gegenbaur) but some of his statements and conclusions should be summarized here.

According to Maurer two types of organs are developed from the integument. The epidermoid organs are those structures which both phylogenetically and ontogenetically arise exclusively from the epidermis, and to which the dermis only enters when necessity for protection or nourishment arises. Here belong the tegumentary sense organs of the lower vertebrates as well as the "pearl organs" of the Teleosts, the femoral pores of the lizards, dermal glands and lastly the hairs of the Mammalia. Integumental organs in the narrower sense are those which have their first foundation in an alteration of the corium and always arise as an elevation of that layer, although the epidermis may be associated with it later and may secondarily acquire great prominence. Here belong the scales of fishes and reptiles, the feathers of birds and certain mammalian scales.

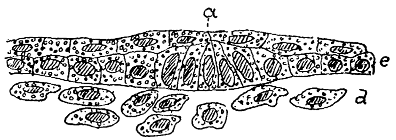

FIG. 14.—Section through the earliest stage of a developing sense organ of *Triton tæniatus*, after Maurer. At *a* the basal layer of the epidermis is changing in character, its cells becoming columnar, the first stage in their conversion into sense cells. Comparison should be made with fig. 1.

From this statement it is clear, if ontogeny be a test, that hair and feathers, are totally different structures; for as we have seen the development of hair begins with the epidermis; that of feathers as clearly with the dermis.

In the first appearance of the hair Maurer sees additional evidence in favor of his view. We have already alluded to the rows in which the earliest hairs are arranged. Maurer finds that the first tactile hairs to appear are arranged in the following rows: (1) supraorbital; (2) infraorbital; (3) zygomatic; (4) angular; (5) upper lip; (6) under lip; and (7) submental; and that these rows follow in a striking way, the course of the tegumentary branches of the tregeminal nerve. The other hairs are not irregularly arranged but are also in regular rows (see fig. 4) and, thinks Maurer, these rows are closely connected with the rows of sensory organs in the Amphibian skin. The grouped arrangement of hairs is secondary and the point of origin of a group is a single hair the follicle of which by budding gives rise to other follicles and hence to the hair group. Such a means of increase is found no where else than in the sensory organs of the Ichthyopsida.

It would be interesting did space permit to go farther into this subject and to take up other tegumentary structures. It is, however, hoped that this brief review will lead to the reading of Keibel's summary already referred to with its bibliography of over one hundred titles.

BIRDS OF THE GALÁPAGOS ARCHIPELAGO: A CRITICISM OF MR. ROBERT RIDGWAY'S PAPER.

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On the 30th of March, Mr. Ridgway published a paper on the "Birds of the Galápagos Archipelago,"[1] in which he makes the following remarks in regard to the genus Geospiza:

"Few genera equal the present one in the extreme modifications in the form of the bill, which in some species (*magnirostris* and *strenua*) is, perhaps, not excelled by that of any

[1] Proc. U. S. Nat. Mus. (No. 1116), Vol. XIX, p. 459-560, Pl. LVI-LVII, Washington, 1896.